

## Response to referees' comments on "SHIMMER (1.0): a novel mathematical model for microbial and biogeochemical dynamics in glacier forefield ecosystems"

We would like to thank the reviewers for their helpful and constructive comments and suggestions, which helped improve the manuscript. We have addressed all concerns that were raised. Please find below our responses to the specific points and questions raised by each referee in blue. Quotes of updated manuscript sections are indicated in red.

### Anonymous Referee 1

In terms of microbial respiration, why do you use the  $Q_{10}$  model, not an Arrhenius equation model? If  $Q_{10}$  is not a constant but depends on soil temperature (Line 26, Page 6169), then it's probably not a representative parameter for the system. But if the reaction rates are modeled based on energetics, for example, using a temperature dependent Gibbs free energy of activation, temperature effects on the metabolic state may be better represented.

Both the Arrhenius, as well as the  $Q_{10}$  model were derived from the same fundamental relationship between temperature and the reaction rate of an elemental chemical reaction formulated by van t'Hoff. Although the Arrhenius and  $Q_{10}$  models are not identical with regard to their mathematical derivation, the  $Q_{10}$  model can be seen as a special case of the Arrhenius equation.

$$\ln Q_{10} = \ln(k_2/k_1) = E_a / R^*(1/T_1 - 1/T_2)$$

Where  $k_1$  and  $k_2$  are the rate constants at temperatures  $T_1$  and  $T_2$ .  $E_a$  is the activation energy and  $R$  the gas constant.  $Q_{10}$  is thus not a constant property of a reaction, but decreases as temperature decreases.

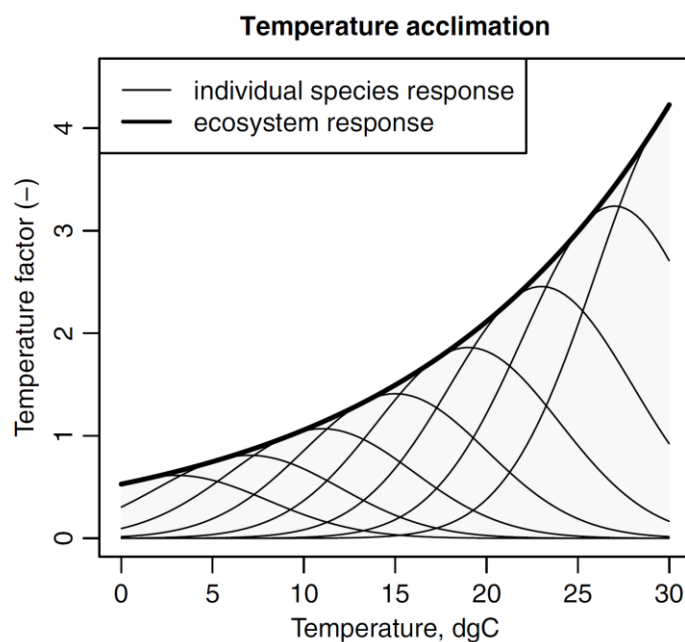
The Arrhenius equation is a semi-empirical formulation used to describe the temperature dependence of the complex multi-step biogeochemical reactions involving a multitude of different organisms and intermediate products. The apparent values for  $A$  and  $E_a$  are generally calculated from rate measurements (although the Arrhenius equation relates the reaction rate constant,  $k$ , and not the rate to temperature). As a consequence, apparent values are an integrative measure of the activation energies of all the elementary reactions that comprise the overall reaction, and is not the activation energy in the thermodynamic sense, but encapsulates the temperature response of the total microbial ecosystem and the organic matter degradability/availability. Therefore, apparent  $E_a$ s show large variabilities between different environments and/or increase/decrease with for instance temperature, substrate bioavailability etc.

Finally, to our knowledge there is no (reliable) relationships linking Gibbs energies to activation energies for anything other than elementary reactions

In summary, we know that reactions rates increase with temperature, but we also know that the environmental details will affect the actual increase in rate. The only thing that makes one way of calculating the temperature dependence of reaction rates versus another (in the absence of data) is that the formulation used to capture this temperature-dependency is relevant to your situation.

The  $Q_{10}$  model, like many other forms of Arrhenius temperature-dependency models and other commonly used temperature functions (see Table 2 in Sierra et al. (2015)), is an empirically derived approximation for temperature response. We decided that the  $Q_{10}$  model was the most appropriate for SHIMMER (1.0) for the following reasons:

- **It represents an ecosystem response.** The typical response of an individual organism to temperature is an increase in metabolic activity to a clearly defined optimum, after which rates decrease. However, the  $Q_{10}$  is more representative of a community response (see below) (Soetaert and Herman, 2009). SHIMMER is not an individual-based model, and groups multiple individuals and species together into six functional groups ( $A_{1-3}$  &  $H_{1-3}$ ). Thus, the  $Q_{10}$  model is appropriate for representing the response of the grouping.



*Response of an ecosystem for individuals (thin lines) and for groups of organisms/ecosystem (thick line) (from Soetaert and Herman (2009))*

- **$Q_{10}$  is a typical measure for soil respiration**, both in field or lab analyses (e.g. Uchida et al. (2002), Tang et al. (2005), Zhou et al. (2013), Zheng et al. (2009)) and in models (e.g. Zhou et al. (2009)). Therefore, it is more familiar among this field of research.
- **We can constrain the  $Q_{10}$  value from previous studies (model and lab), and compare it with our own lab-derived value.** It is known that the  $Q_{10}$  value varies depending on the environmental characteristics of the system of interest (Xu and Qi, 2001; Zhou et al., 2009). We have based the  $Q_{10}$  formulation on existing modelling and field/lab studies, which we have used to inform the parameter value (Uchida et al., 2002; Schipper et al., 2014; Soetaert and Herman, 2009; Yoshitake et al., 2010). Furthermore, we plan to use lab techniques on samples collected from the field to narrow the plausible range for this parameter for the specific field site of interest (this will be part of a future publication). The  $Q_{10}$  formulation is therefore appropriate because we can directly compare our lab-based calculation with previous attempts to characterise this response.

- **It is appropriate for the level of detail resolved by the model.** If the model resolved finer detail (molecular and chemical processes), then an intrinsic temperature sensitivity (i.e. theoretic rates determined by molecular structure e.g. Gibbs free energy) may be appropriate. However, for the SHIMMER model formulation, the apparent temperature sensitivity (with appropriate environmental constraints caused by heterogeneous soil properties) formulated with a  $Q_{10}$  function over a typical temperature range is sufficient. The plausible range for  $Q_{10}$  in SHIMMER is partly informed by macro-molecular thermodynamic theory for low temperature ecosystems (Schipper et al., 2014), thus showing how energetics theory can inform the dynamics of simpler model approximations and formulations.
- **The  $Q_{10}$  formulation is simple** enough that it can be fully tested in the sensitivity and uncertainty evaluation.

This model is a 0-D model, which does not resolve transport driven by spatial gradients or advection. While this is probably sufficient for in situ soil processes because of the presumed homogeneity and shallow soil depths, it may have neglected vertical aqueous transport of carbon and nutrients if there is surface runoff. Would this bias the model results?

The referee has raised a valid point regarding transport driven by spatial gradients or advection. The model is 0-D, and as such, spatial and vertical gradients and advection are not resolved explicitly. Instead, vertical transport is simplified: an input flux ( $I$ ) and a leaching flux ( $W$ ) is modified by a parameter  $\nu$  on behalf of the retention of nutrients in the surface layer. The aqueous flux of carbon and nutrients in surface (and sub-surface) runoff is thus represented as  $(I * (1-\nu))$ . Currently, the quality of observational data does not justify an explicit representation of depth, advection and diffusion. This is due to a lack of depth data, information to constrain input and output fluxes, and physical aspects crucial to advection and diffusion (e.g. soil moisture) throughout the season. However, future improvements in observations and model design may facilitate this development in the next version of SHIMMER.

What is the mechanism for the oscillations in the biomass of soil autotrophs and nitrogen fixing autotrophs in Figure 6? Is it possible that they are artefacts from numerical evaluation?

The oscillations in biomass of soil autotrophs ( $A_2$ ) and nitrogen fixing autotrophs ( $A_3$ ) are mainly due to the seasonal variation in solar radiation and to a lesser degree to seasonal changes in soil temperature and nutrient input/availability, and are not numerical artefacts or the result of non-linear dynamics. Such oscillations are well documented by observational data indicating an increase in biomass (e.g. cyanobacteria and other (mostly photosynthetic) organisms) in high-latitude soils during the summer (see e.g. Jefferies et al. (2010)). Summers are characterised by high solar radiation, whilst in the winter a layer of snow prohibits nearly all solar radiation from reaching the soil surface. Other organisms ( $A_1$  and  $H_1-3$ ) are not sensitive to light and have a much smaller seasonal oscillations in biomass.

Why is the seasonal amplitude in simulated total microbial biomass at the Damma Glacier (Figure 10) much larger than that at the Athabasca Glacier (Figure 11)?

Major differences in the set-up between the Damma and Athabasca glacier systems are:

- *Initial conditions*: Damma Glacier has higher initial biomass, carbon substrate and nutrient concentrations than the Athabasca Glacier.
- *Allochthonous input*: Substrate input is much greater at the Damma Glacier ( $v_{Sub} = 0.6$ ) compared to the Athabasca ( $v_{Sub} = 0.05$ ).

The seasonal oscillations are reduced at the Athabasca Glacier due to scarcity of nutrients, thus inhibiting maximum growth rates and slowing the biotic response to seasonal variability. There is a lower accumulation of biomass and nutrients at the Athabasca Glacier. Accordingly, lower biomass yields smaller seasonal oscillations because there is less biomass to respond to the change. The manuscript text has been adjusted accordingly to highlight the referee's point and suggest causal mechanisms for the differences in seasonal oscillations:

**“The seasonal oscillations in microbial biomass and activity at the Athabasca Glacier forefield are considerably smaller than the Damma Glacier forefield, due to increased nutrient scarcity (inhibiting growth and slowing the biotic response to seasonal variability) and lower microbial biomass.”**  
(Section 5.4.2).

For the Damma Glacier, the model tends to stabilize in terms of the total microbial biomass and DIP, and increase slowly in C substrate and ON, while the data show roughly exponential increases for all the variables (Figure 10). This discrepancy is attributed to vegetation onset. But why doesn't it happen at the other site? What would explain such difference? Does it mean that the model is not applicable to the later stages of soil development in such ecosystem when vegetation occurs?

*At the Damma Glacier*: biomass, bacterial production and DIP stabilize while there is a continual increase in C substrate, ON and OP. We attribute this to the rapid exhaustion of carbon substrate (sustaining a lower rate of microbial activity, heterotrophic decomposition of organic carbon, and therefore DIP liberation), as suggested in the manuscript:

**“A high proportion of labile substrate (39.4 % in year 1) supports high rates of heterotrophic production and rapid accumulation of heterotrophic biomass. Labile substrate is rapidly depleted (Fig. 12a) followed by a sharp decline in biomass (Fig. 10). Following the exhaustion of labile organic carbon substrate, heterotrophic production is sustained at a rate of roughly  $10.0 \mu\text{g C g}^{-1} \text{ yr}^{-1}$  and predicted microbial biomass is within the natural variability of the observational data”** (p6175, line 25)

*At the Athabasca Glacier*: We do not see this stabilization. Rather, biomass, bacterial production and DIP continue to increase. This is due to a continued accumulation of labile substrate (as opposed to a rapid exhaustion), which is able to support an increasing level of microbial production.

We have edited the manuscript to make this clearer:

**“A high level of bacterial production is sustained by a continuous pool of labile substrate.”** (Section 5.4.2.)

The onset of vegetation is not resolved within the model. The referee correctly notes that the model is not applicable to the later stages of soil development in an ecosystem where vegetation establishes rapidly. We express this limitation in the manuscript:

“SHIMMER does not explicitly account for vegetation and thus cannot reproduce the high organic carbon accumulation in vegetated sites (Fig. 10).” (p6179, line 25)

Line 6–8, Page 6148: “Many of their parameters cannot be constrained on the basis of information available for glacier forefield ecosystems” I wonder what those parameters are. Are physical, biochemical or physiological parameters that are difficult to constrain for glacier forefield? Please name a few of them.

There is confusion here in the original text. In fact, many of the parameters (such as half-saturation constants ( $K_s$ ), growth rates ( $I_{max}$ ), growth efficiencies ( $Y$ )) can, and are translated to the SHIMMER model for glacier forefields. The specific nature of the glacier forefield system as a whole, rather than the parameters, prohibits the use of existing models, and warrants the development of a new model. We acknowledge that the original wording in the manuscript is not clear, and we have edited this paragraph to express this point more clearly and succinctly:

“Forefield ecosystems are characterised by extreme and highly variable environmental conditions and rapidly changing compositions of microbial communities whose interplay results in unique chronosequence dynamics (Bradley et al., 2014). There is not a single model that can represent the unique forefield development without an unacceptable level of abstraction and simplification of the system.” (Section 1. Introduction)

Line 17, Page 6148 to Line 17, Page 6150: I think there are a lot of overlapped information between these two paragraphs and Table 1. Please consider abridge them and try to be concise. Or maybe move some information to the model description section. It’s not necessary to be overly elaborate on the model construction in the introduction.

The manuscript has been modified. Some text has been omitted to make this section more concise.

Line 25, Page 6152: Define “EPS” here. You don’t want your readers to look it up from other papers.

Agreed, text changed accordingly.

Line 12, Page 6153: Please define “L” in Eq. (4) as PAR.

Agreed, text changed accordingly.

Line 27, Page 6154: “Nitrogen fixation in the SHIMMER model is sensitive to many of the environmental factors often cited in the literature, including surrounding DIN concentrations, temperature, and carbon and phosphorus limitation (Liu et al., 2011).” I haven’t seen an equation describing such dependence in the paper. The production term in Eq. (13) does not have DIN dependence or phosphorus dependence. So which equation does this sentence refer to?

This sentence refers to the following equations in Table 4:

- Growth of  $A_3$  with nitrogen fixation ( $U_{A3\_N2}$ )
- Growth of  $H_3$  from labile substrate and nitrogen fixation ( $U_{H3L\_N2}$ )
- Growth of  $H_3$  from refractory substrate and nitrogen fixation ( $U_{H3R\_N2}$ )

The text has been edited to direct the reader directly to the equations of interest.

- Line 7, Page 6156: typo, “dependant” → “dependent”

Agreed, text changed accordingly.

Line 10, Page 6156: Why do you assume that the loss terms are proportional to the square of the biomass? I don't see a citation here. Please justify your assumption with one or two sentences.

Microbial death is poorly defined empirically, and as such there are many possible formulations of death rates. We have added an explanatory sentence:

“Mortality due to predation is usually density dependant (Kaitala et al., 1999; Levin, 1998). Accordingly, loss terms ( $G_{Ai}$  and  $G_{Hi}$ ) are density dependent and are also sensitive to variations in...”

Eqs. (11) and (12), Page 6157: Please define the  $v_{sub}$  parameter here, though it has been described in Table 5.

Agreed, text changed accordingly.

Line 19, Page 6157: What are the N/C and P/C ratios used here? If the values are only shown in Table 5, then you need to guide the readers to Table 5.

Agreed, text changed to direct readers to Table 5.

Line 7, Page 6158: Could you specify which version of the R language you were using? It may not make a difference between versions, but it'll be good to provide such information, just in case.

The model can be run on any recent version of R. We decided not to include a version number, since the user is not required to have specific system specs or versions to run the code. We have added a supplementary package containing the model source code and a “Read Me” guide containing information on set up and required packages.

Line 7, Page 6159: The extinction coefficient has a unit  $m^{-1}$ , so it has to be  $6 m^{-1}$ .

Agreed, text changed accordingly.

Line 19, Page 6161: "The calculation of may yield a 'false-negative' result (i.e. a value close to zero) when the variation in model output either side of the nominal value has an opposite sign (i.e. a parabolic relationship between the parameter value and model output)." I'm not sure I understand what you try to mean by this sentence. If you have a parabolic shape relationship, does it not mean that the parameter has an optimum value within that range? Why would it be an unwanted behaviour? And if you want to detect the "false-negative" behaviour, why not look at the second-order derivative?

Agreed that this is not clear in the submitted manuscript. This section has been re-worded, and an additional figure (Fig. 5) has been included to illustrate the point.

"Model output is assessed graphically for each parameter (e.g. Fig. 6). Firstly, the shape of the model output variation is assessed to see if the value for  $\lambda$  is representative of sensitivity. An unrealistic  $\lambda$  may be calculated if the nominal parameter is near a vertex and the variation in model output either side of the nominal value has an opposite sign (i.e. a parabola). This is illustrated in Fig. 5b, whereby  $\delta X$  is low, and thus a low  $\lambda$  value obtained, even though the sensitivity is relatively high (i.e.  $X$  depends strongly on  $p$ )."

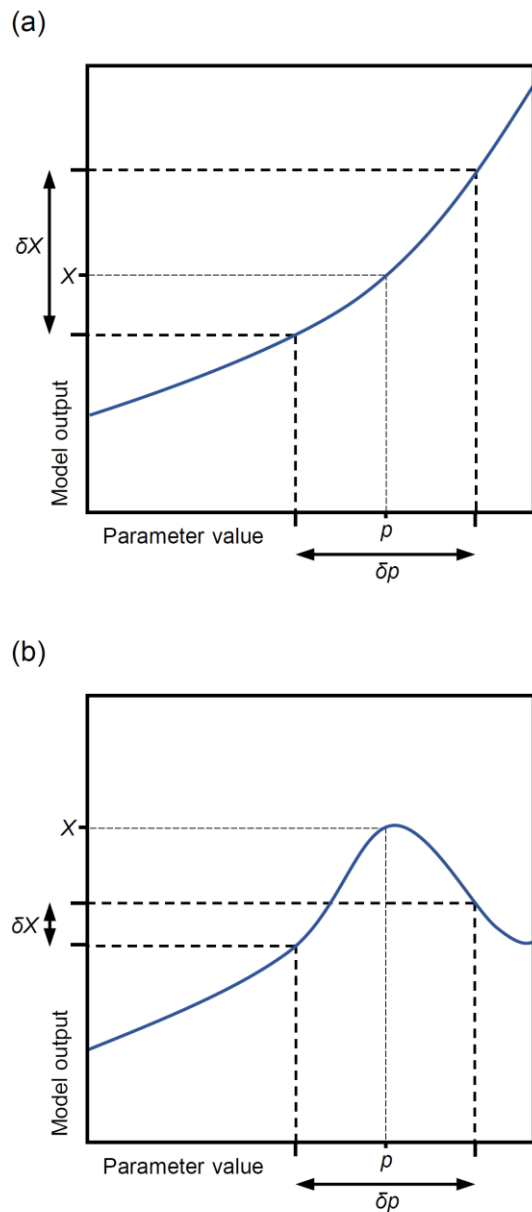


Figure 5. Illustration of calculation of sensitivity ( $\lambda$ ) where (a) the value of  $\lambda$  is representative of the sensitivity (b) the value of  $\lambda$  is not representative of the sensitivity. In (b) the apparent sensitivity ( $\lambda$ ) will be low due to model behaviour either side of the nominal parameter value having an opposite sign, even though the model may be truly sensitive to that parameter.

Line 22, Page 6164: “high plat abundance” Is there a typo? Do you mean “plant abundance” or “microbial mat abundance”?

Typo, text changed accordingly.

Line 4, Page 6165: “and initial substrate bioavailability is assumed to be 40% labile and 60% refractory” The initial substrate bioavailability for the other site is assumed “30% labile and 70% refractory”. Is there any explanation for the difference?



This is a mistake in the text. Initial conditions for both sites assume 40% labile and 60% refractory (correctly displayed in Table 2, below). The text has been changed accordingly.

**Table 2.** State variables and initial values.

State Variable	Units	Description	Damma Glacier, Switzerland	Reference	Athabasca Glacier, Canada	Reference
$A_1$	$\mu\text{g C g}^{-1}$	Subglacial chemolithoautotrophs	0.617	Bernasconi et al. (2011)	0.950	Insam and Haselwandter (1989)
$A_2$	$\mu\text{g C g}^{-1}$	Soil autotrophs	0.617	Bernasconi et al. (2011)	0.950	Insam and Haselwandter (1989)
$A_3$	$\mu\text{g C g}^{-1}$	Nitrogen fixing soil autotrophs	0.617	Bernasconi et al. (2011)	0.950	Insam and Haselwandter (1989)
$H_1$	$\mu\text{g C g}^{-1}$	Subglacial heterotrophs	0.617	Bernasconi et al. (2011)	0.950	Insam and Haselwandter (1989)
$H_2$	$\mu\text{g C g}^{-1}$	Soil heterotrophs	0.617	Bernasconi et al. (2011)	0.950	Insam and Haselwandter (1989)
$H_3$	$\mu\text{g C g}^{-1}$	Nitrogen fixing soil heterotrophs	0.617	Bernasconi et al. (2011)	0.950	Insam and Haselwandter (1989)
$S_1$	$\mu\text{g C g}^{-1}$	Labile carbon substrate	278.520	Bernasconi et al. (2011)	117.720	Insam and Haselwandter (1989)
$S_2$	$\mu\text{g C g}^{-1}$	Refractory carbon substrate	417.780	Bernasconi et al. (2011)	176.580	Insam and Haselwandter (1989)
DIN	$\mu\text{g N g}^{-1}$	Dissolved Inorganic Nitrogen	0.160	Brankatschk et al. (2011)	0.070	Stoichiometric
DIP	$\mu\text{g P g}^{-1}$	Dissolved Inorganic Phosphorus	0.500	Bernasconi et al. (2011)	0.210	Stoichiometric
$ON_1$	$\mu\text{g N g}^{-1}$	Labile nitrogen substrate	39.440	Bernasconi et al. (2011)	16.600	Stoichiometric
$ON_2$	$\mu\text{g N g}^{-1}$	Refractory nitrogen substrate	59.160	Bernasconi et al. (2011)	24.900	Stoichiometric
$OP_1$	$\mu\text{g P g}^{-1}$	Labile phosphorus substrate	23.120	Stoichiometric	9.770	Stoichiometric
$OP_2$	$\mu\text{g P g}^{-1}$	Refractory phosphorus substrate	14.660	Stoichiometric	14.660	Stoichiometric

Line 27, Page 6165: “When considering a 1 cm deep soil profile, 1 g dry soil occupies a surface area of 0.869 cm<sup>2</sup>.” This means exactly that the dry density of the soil is 1.15 g cm<sup>-3</sup>. Then why repeat the information if you have stated it in the preceding sentence? Also, you may need to say “the typical dry density of the soil”, because “density” usually means bulk density not dry density.

Agreed, text changed accordingly.

Table 1 on Page 6196: This table looks a bit too wordy since many aspects are already explained in detail in the main text. Better abridge the description of each entry down to two sentences/lines.

Agreed, Table 1 has been considerably shortened.

Table 2 on Page 6197: I think it’s better to call  $A_2$  and  $H_2$  “generic soil auto-/heterotrophs” or “non N<sub>2</sub>-fixing soil auto-/heterotrophs”.

Agreed, text changed accordingly.

Figure 4 on Page 6207: The unit of the ordinate in panel (a) should be shown as “W m<sup>-2</sup>”

Agreed, figure changed accordingly.

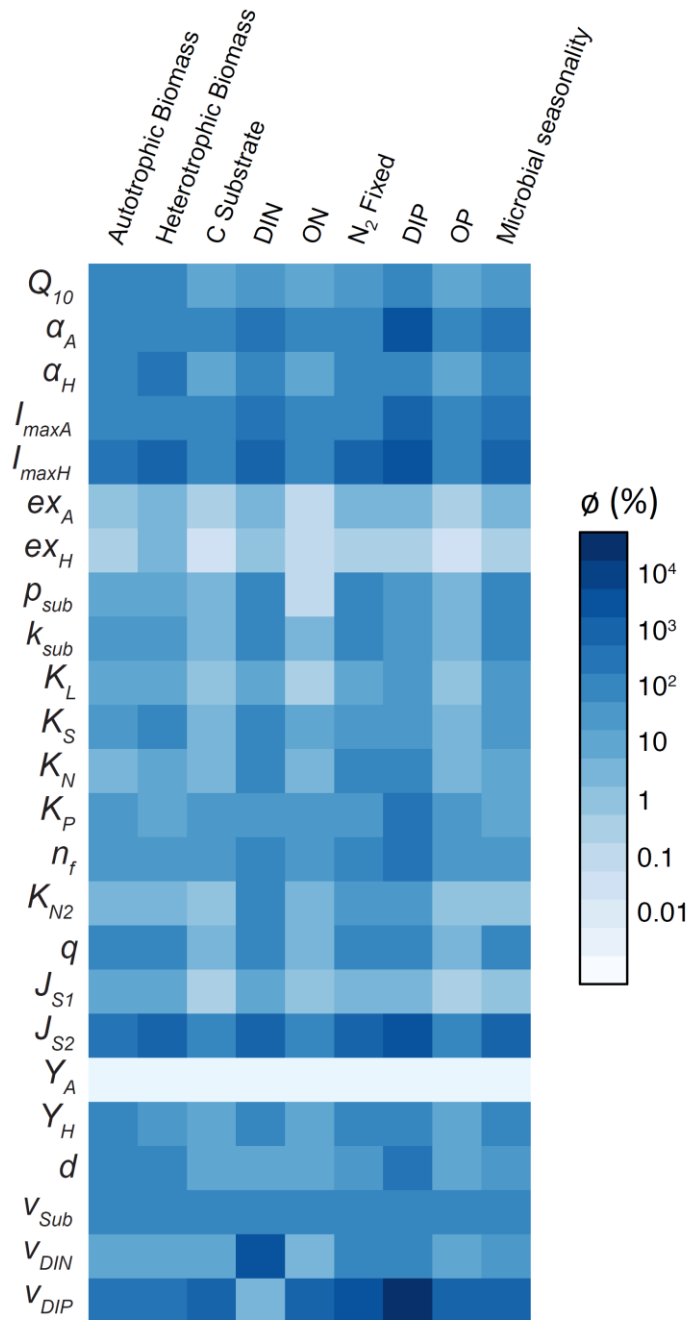
Figure 7 on Page 6210: It is very hard to see clearly the variable names on the ordinate, unless zoomed to 200% and above. For better visualization, I suggest the authors replot this figure as a heat map. Juxtapose the nine parameters as the abscissa, and choose a color bar that is distinct enough and colorblind-safe for the variation in.

We appreciate that the variable names in Figure 7 in the *Discussions* paper are difficult to read due to the compressed landscape format. However, the final paper will be in portrait format and we will make sure in the production process and proof version that all labelling is clear and legible.

We have plotted Figure 7 as a bar plot because there this form of presentation provides more information to the reader. Due to the differences in the magnitude of sensitivity between model outputs, much of the detail in some less sensitive but nevertheless important model outputs / parameters would be lost if normalised to a single colour scale.

Figure 9 on Page 6212: This figure has the same technical problem as Figure 7. Better replot it as a heat map, and perhaps use a logarithmic scale colorbar for  $\phi$  given its highly variable range. Also, please specify that  $\phi$  is a percentage value by adding “%” as its unit.

We have re-plotted this figure as a heat-map. Whilst valuable detail/information would have been lost from the sensitivity plot, this is not the case with the uncertainty (if it is plotted as a logarithmic scale).



“Heat-map showing uncertainty of model outputs ( $\phi$ ) arising from individual parameters. The model is forced with meteorological data from the Damma Glacier (Fig. 4) over 75 years.”

### Anonymous Referee 2

This manuscript presents a model for the development of microbial communities and biogeochemical dynamics in forefield ecosystems. The focus of the model on the early development of primary successions makes it interesting and of potential application to other early successional

environments. I think this is an important contribution and recommend publication after some minor issues are addressed.

Although I found the split of the microbial community between different groups of autotrophs and heterotrophs interesting, I'm also concerned that this approach leads to a high degree of complexity due to the nonlinearities of the system of ODEs. The provided figures seem to indicate that the model converges to a steady-state, but it's this steady-state unique? Is it possible to obtain multiple steady-states? Given the non-linearities in the model I would expect possible bifurcations. Have you looked at this aspect?

The referee has picked up on a very interesting point. Unfortunately, the analyses of non-linearities and bifurcations in the model is beyond the scope of the model description paper. However, we are currently exploring these aspects. It is likely that the non-linearities in the model will lead to bifurcations. In addition, the evolution of the forefield will depend largely on the initial conditions (year 0) and changes in external forcing associated to ongoing climate change may lead to the crossing of thresholds/ tipping points and fundamentally different behaviour.

Similarly, due to the nonlinearities in the model, the output variables tend to oscillate. Are these oscillations realistic? Can you say something about what parameters may lead to these oscillations? It may be useful to look at the analyses in Manzoni & Porporato (2007, Soil Biol Biochem 39: 1542) and Wang et al. (20014, Biogeosciences 11:1817).

See answer to Referee 1.

In general, this manuscript is too long. I think you can do a favor to the reader by removing unnecessary parts from all sections. Even the abstract is too long. Section 6 can be easily merge into two or three paragraphs without losing much content.

We acknowledge this point and have further shortened the manuscript.

Although the authors mention that the source code is available upon request, it'd be much better if the code is available in a public repository. Would it be possible to upload the source code to GitHub or other public repository?

We agree with this point, and have made the SHIMMER source code available as a supplementary package together with a Read Me file. The "Code Availability" text has been edited accordingly:

The SHIMMER source code related to this article is provided as a supplementary package together with a Read Me file. The code is written and executed in the free open source computing environment and programming language R, which is available for download on the web (<http://www.r-project.org/>).

-Page 6152: Are DIN and EPS previously defined?

Agreed, text changed accordingly.

-Page 6176, line 6. pattern.

Agreed, text changed accordingly.

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